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UCA MARGUERITA, A NEW SPECIES OF FIDDLER CRAB (BRACHYURA: OCYPODIDAE) FROM EASTERN MEXICO¹

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Abstract.—A species of fiddler crab new to science, Uca marguerita, on the eastern terrigenous coastline of Mexico is reported. Previously, several specimens of the newly described species were confused with either Uca virens Salmon and Atsaides, Uca burgersi Holthuis, or Uca speciosa Ives. A detailed morphological description of adult specimens along with a general description of the male's courtship display is presented. The new species is compared with sympatric congeners. On both morphological and behavioral grounds, Uca marguerita appears to be a member of the subgenus Minuca of Crane (1975).

Several authors have reviewed the North American fiddler crabs. However, only Rathbun (1918), Buitendijk (1950), and Crane (1975) have reported new records from the east coast of Mexico. Rathbun identified *Uca mordax* Smith in collections from Tampico, Mexico. Buitendijk also believed *U. mordax* as well as *U. speciosa* Ives were present in the Mexican state of Veracruz. Recently, Holthuis (1967) and von Hagen (1970) considered Buitendijk's *U. mordax* records to be *Uca burgersi* Holthuis. In a major taxonomic revision, Crane reclassified Rathbun's Mexican specimens as either *Uca vocator* Herbst, *Uca spinicarpa* Rathbun or *Uca pugnax virens* Salmon and Atsaides. Simultaneously, she also added 20 new specimens which she believed to represent *U. p. virens* from southern Veracruz. These gifts to the New York Zoological Society extended the presumed range of *Uca virens* from the area between Ocean Springs, Mississippi, and Port Aransas, Texas (Salmon and Atsaides, 1968), into southeast Mexico. *Uca rapax* Smith was also recognized to range as far north as Tamaulipas.

The taxonomic assessments of both Crane (1975) and Holthuis (1967) are based on examination of a few preserved museum specimens from eastern Mexico. In addition several authors have expressed the opinion that the original type characteristics for *Uca virens* as well as *Uca longisignalis* Salmon and Atsaides are unreliable (Crane, 1975:203; von Hagen, 1975, 1980). On the one hand, Crane tentatively proposed five traits to distinguish

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U. virens from other Minuca but felt her choice to be marginally acceptable without a more complete collection series. On the other, von Hagen's (1980) approach has been to synonymize the newer species with older, traditionally described taxa. Complete resolution of this controversy is beyond the scope of the present study. However, as a result of field collections and examination of available preserved museum specimens, it is apparent that Crane's difficulty in obtaining reliable traits for U. virens arises from the simultaneous treatment of at least two species. Part of the U. pugnax virens as well as some of the U. burgersi and U. speciosa from eastern Mexico are members of an undescribed species. This new species, Uca marguerita, is limited to the terrigenous areas of eastern Mexico. It does not occur in the United States or upon the biogenic soils of the Yucatan peninsula.

Materials and Methods

Populations of fiddler crabs in the western and southern Gulf of Mexico were studied during December 1972, September 1974, March 1976 and September 1976. More than 3000 specimens were collected from 77 localities between Ocean Springs, Mississippi, and Chetumal, Quintana Roo, Mexico. Two hundred thirteen individuals of the new species were found in localities between the states of Tamaulipas and Campeche, Mexico. From these collections, lots were deposited in the USNM, Department of Invertebrate Zoology, Washington, D.C. Samples of the new species were supplied from Tamaulipas, La Pesca; Veracruz, Rio Panaco; Veracruz, La Barra; Veracruz, Nautla; Veracruz, Laguna La Mancha; Veracruz, Boca del Rio; Tabasco, Puerto Ceiba; Tabasco, Frontera; Campeche, Rio San Pedro. The specimens from Laguna La Mancha in Veracruz are designated as male holotype (USNM 180400) and female allotype (USNM 180401). The remainder (USNM 180443 through 180450) are designated as paratypes. In addition, older preserved materials also were examined. The following Min*uca* were made available by the USNM:

Uca burgersi Holthuis 1967—138490 (Belize), 139173 (Belize), 13488 (Florida).

Uca longisignalis Salmon and Atsaides 1968—121599 (Holotype) 122204 (Paratype), 2259 (Grand Isle), 21845 (Biloxi), 33035 (Matagorda), 72132 part (Texas), 74902 (Ocean Springs), 122764 (Yankeetown), 138647 (Yankeetown), 138648 (Galveston).

Uca minax (LeConte 1855)—42618 (Sarasota), 64083 (Ft. St. Phillip), 64155 (Grand Isle), 98144 (Lake Pontchartrain).

Uca mordax (Smith 1870)-18430 (Swan Island), 50950 (Belize).

Uca pugnax (Smith 1870)—17488 (Winyah Bay), 71196-7 (Ft. Macon), 74455 (Brigantine).

Uca rapax (Smith 1870)—15057 (Mobile Bay), 25033 (Matagorda), 95526 (Yucatan), 96475 (Laguna Madre).

Uca virens Salmon and Atsaides 1968—121598 (Holotype), 122205 (Paratype), 30570 (Cameron), 33031 (Matagorda), 72132 (Texas), 122765 (Port Aransas), 72131 (Texas), 138642 (Corpus Christi), 138643 (Port Aransas), 43353 (Tampico), 138644 (Veracruz), 138645 (Veracruz), 18689-dry (Tampico).

Uca vocator (Herbst 1804)—21373 (Belize), 138855 (Veracruz), 139175 (Tampico).

The following lots were made available by the Rijksmuseum:

Uca burgersi Holthuis 1967-7577 (Veracruz), 7578 (Veracruz).

Uca speciosa (Ives 1891)-7574 (Veracruz).

A number of morphological characteristics were measured in order to characterize the new species. Measurements were taken to the nearest 0.05 mm with a vernier caliper. Carapace breadth was measured at maximal distance between anterior dorsolateral margins. Body length was taken from the front of carapace to posterior margin above abdomen. Frontal width was taken between the inner junctions of the eyebrows with the lower frontal margin of the carapace. The length and width of the merus was measured along the respective central axis of the fourth ambulatory segment. Propodal ratios were obtained from measurements taken on the fifth segment of the ambulatory. The details of gonopodium and gonopore structures were studied with the aid of a stereo dissecting microscope.

The cheliped waving behavior of male fiddler crabs was recorded in the field using a 16 mm movie camera where ambient temperatures were always above 25°C. General wave form and temporal components of the courtship display were determined by frame analysis. Since this behavior was recorded at either 16 or 24 frames per second, estimates of temporal characteristics were determined by multiplying the number of frames involved by either 0.0625 or 0.0416 seconds for respective recording speeds.

Results

Uca marguerita, new species Figs. 1, 2

Uca mordax.-Rathbun, 1918:391-393 [part].

Uca mordax.—Buitendijk, 1950:279 [part].

Uca speciosa.—Buitendijk, 1950:279 [part].

Uca burgersi.—Holthuis, 1967:51–54 [part].

Uca burgersi.-von Hagen, 1970:225 [part].

Uca speciosa.-von Hagen, 1970:227 [part].

Uca pugnax virens.—Crane, 1975:200–205 [part].—not Uca virens Salmon and Atsaides, 1968.

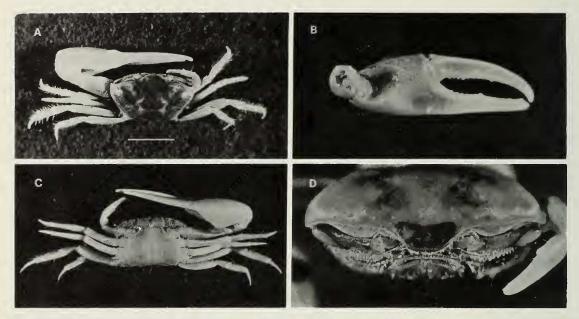


Fig. 1. Uca marguerita: A, Dorsal view; B, Inner surface of male cheliped; C, Ventral view; D, Frontal view of interocular region. White bar = 1 cm.

Type-locality.—Mexico, Veracruz, Laguna La Mancha (19°40'N, 96°20'W) between Villa Rica and Cardel. In addition to the USNM paratypes, examples from the following lots have been identified as *Uca marguerita*: USNM 43353 part, USNM 138644, USNM 138645, RMNH 7574 part, RMNH 7577 part, and RMNH 7578 part.

Diagnosis.—Fig. 1. Width of rounded frontal lobe less than ¹/₃ maximum carapace width. Ventral margins of distal ambulatory segments without pubescence. In males, superior carina above carpal cavity in palm of cheliped consists of a row of tubercles. Distal end of this carina turned forward toward dactyl. In females, genital operculum without prominent tubercle.

Etymology.—Marguerita a common christian name used in the endemic region of the crab.

Morphological description.—From dorsal view (Fig. 1A), carapace length 66.0% or less of breadth. Carapace widest slightly posterior to anterior margins. Largest male 24.7×15.1 mm; largest female 17.3×12.0 mm at Nautla, Veracruz. Surface finely granular and pitted in both sexes. Females have few large tubercles in epibranchial regions. Neither pubescence nor numerous setae on dorsal carapace. H-depression in cardiac-mesogastric region very prominent. Color in preserved specimens homogeneously dark except for occasional concentration in depression. Carapace of living specimens brown, dark green, or gray. Frontal lobe between eyestalks less than 33.0% of maximum carapace width (Fig. 1D); in males near 27%, in females near 31%. From dorsal view, frontal lobe distinctly rounded or spatulate

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and very shallow. Maximum width of eyebrow almost equal to diameter of adjacent eyestalk peduncle. Distal cornea occupies between 25 and 33% of peduncle length. Anterior margins finely granular in both sexes. Sulcus posterior to eyebrow forms deep transverse depression curving toward mesogastric region. Anteriorly, dorsolateral margins of carapace curving inward slightly. Junction of anterior and posterior forming curved but obtuse angle. Posteriorly lateral margins converging toward midline of carapace giving body shortened appearance.

When carapace is viewed from anterior (Fig. 1D), lobed interocular region very shallow and rounded. Carapace moderately arched through axis of width. From lateral view, carapace strongly convex, almost subcylindrical. Eyebrows strongly inclined horizontally.

Outer and upper manus of cheliped covered with very large tubercles. Dorsal margin distinctly tuberculate. Ventral margin of manus with tubercles forming a distinct keel. Submanus sulcus prominent. Tubercles of outer manus becoming minute on pollex. Both pollex and dactyl flattened, more bladelike than tubular (Fig. 1B). Pollex with 3 rows of tubercles in gape. Usually 1 large tubercle or "tooth" more than halfway along pollex in gape. Three to 5 tubercles at distal end of pollex. Tip thick. Pollex with 4 or 5 large tubercles on ventral margin of dactyl-propodus articulation that do not traverse from outer to inner pollex surfaces. Dactyl with teeth in gape. Upper margin of carpal cavity on inner manus lined with a prominent ridge of tubercles or superior carina (Fig. 1B). Some pubescence may be present in cavity. Distal end of carina turned distinctly toward dactyl as it approaches palm. Region dorsal to end of carina forming a smooth, triangular sulcus. Ventral manus with oblique tuberculated ridge extending about 34 distance to pollex. Distally, this consists of 2 or 3 ill-defined rows of smaller tubercles. Proximately, these converge into a prominent, elevated apex consisting of larger tubercles at ventral border of carpal cavity. Apex vertical to surface of palm. From apex, a row of tubercles follows outer edge of carpal cavity and extends upwards, almost intersecting with superior carina. Proximal palm covered with numerous large tubercles equal in size to those on oblique ridge. Palm area appears swollen because of deep sulcus at intersection of pollex and high apex of oblique ridge. Two rows of tubercles near dactyl articulation: one row on predactyl ridge, other more proximal to palm. Proximal row divergent from distal with dorsal end curving toward dactvl.

Form of minor cheliped similar to that of other *Minuca*. Distal end of pollex and dactyl sparsely setose. Usually fewer than 10 short hairs on either finger. Serrations in gape weakly developed. Distal end of merus with a few long setae parallel to dorsal propodal articulation.

Dorsal margins of ambulatory merus slightly convex. Both anterior and posterior surfaces covered with short setae. Merus of third ambulatory

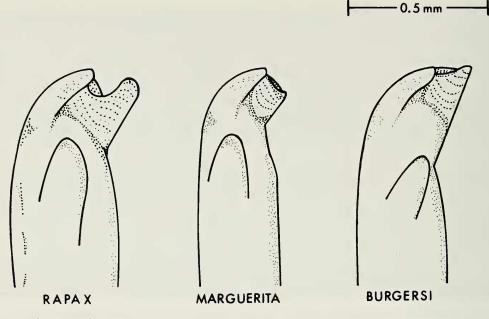


Fig. 2. Gonopodium structures of *Uca rapax* Smith, *Uca burgersi* Holthuis and *Uca marguerita* from eastern Mexico. Anterior view of right gonopodium from males of carapace widths 17 to 18 mm. $60 \times$.

about 2.56 times longer than wide in males and about 2.22 times in females. Ventral surface of first, second, and third meri with numerous setae but no pubescence (Fig. 1C). Usually at least 5 setae per merus. Fourth leg with 0 to 5 setae per merus. Propodal and carpal segments of first 3 ambulatories with pubescence only on dorsal surfaces. Occasionally pubescence present on fourth ambulatory propodus and carpus, more frequent in females than males. Numerous long setae present in rows on anterior, posterior, dorsal and ventral surfaces of propodus. Two rows on dorsal surface. Propodus width about 30% of length on first ambulatory in males.

Copulatory pleopods of male thin and nearly straight when viewed from sternum. After terminal setae are removed, distal end appears constricted before angling of tip (Fig. 2). Tip turned almost to right angle with lateral margins of carapace. Distal tip with small shield-shaped cuticular process. Free edge smooth and undeveloped. Two soft palps present. One subterminal near constriction extending distally to near origin of cuticular process. Second palp terminal on inner lateral surface with distal end embracing cuticular process. Figure 2 compares tip of nude gonopodium of *Uca marguerita* with those of *U. burgersi* and *U. rapax* of comparable size. These differences appear consistently across the range of the new species. Female gonopore without tubercle. Operculum lined with thin rim from sternum. Anterior margin may show small microscopic fold with edge protruding toward center of operculum.

Geographical distribution.-The new species was collected in brackish

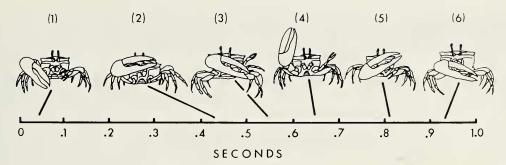


Fig. 3. High intensity courtship display in male *Uca marguerita*. Major positions of cheliped indicated by parentheses. (See text.)

habitats between La Pesca, Tamaulipas, and Rio San Pedro, Campeche, Mexico. The specimens reported as *Uca pugnax virens* from Mexico (Crane, 1975; USNM 43343 part, 138644 and 138645) belong to the new species. The additional 16 specimens from Rio Tonchochapa could not be located. Holthuis (1967) and von Hagen (1970) both consider the entire lots RMNH 7577 and 7578 to be *U. burgersi* from Veracruz. One male from RMNH 7577 (Nautla) and 3 males and 1 female from RMNH 7578 (Casitas) are *Uca marguerita*. The clawless male from *U. speciosa* lot RMNH 7574 is also the new species (Casitas). The new species thus appears to be endemic to the western shores of the Bay of Campeche.

Male courtship display.—The cheliped waving of the new species has been recorded at two localities within its geographic range. Temporal and topological components of this supplementary characteristic are useful for distinguishing the new species in the field and aiding in the determination of phylogenetic affinities. Thirty waves from seven males at La Pesca, Tamaulipas, and Puerto Ceiba, Tabasco, were studied by frame analysis.

The form of the wave in the new species is relatively simple and appears consistent between northern (n = 2) and southern (n = 5) males. As illustrated in Fig. 3, the heel of the cheliped (proximal manus) and carpus are raised to a level near the front of the carapace (position 1 and 2). The fingers of the claw then follow and are held momentarily at the carapace front (position 2). At this point, the axis of the manus and dactyl are more or less parallel with the substrate. The cheliped is oscillated laterally while in this position (3). The propodus is then quickly flexed vertically through a vertex (position 4) and downward (position 5) to a frontal position (6). There is no apical pause but the cheliped is rotated slightly exposing the inner manus during the apical transition. On the rapid return or downstroke, the fingers of the claw do not touch the substrate. Also during the descent phase, the proximal carpal segment is lowered before the distal manus and dactyl (position 5).

The singular frontal pause appears to be characteristic of the wave. Only

Type of wave	No.	Mean duration (sec) SE	Heel to hold (sec) SE	Pause (sec) SE	To apex (sec) SE	Return (sec) SE
High	6	0.92 ± 0.14	0.41 ± 0.05	0.14 ± 0.05	0.12 ± 0.08	0.28 ± 0.10
Moderate	19	1.54 ± 0.21	0.76 ± 0.22	0.19 ± 0.09	0.23 ± 0.09	0.38 ± 0.14
Low	5	$2.63~\pm~0.61$	1.66 ± 0.57	$0.32~\pm~0.13$	$0.18~\pm~0.09$	0.37 ± 0.18
					0.18 ± 0.06	0.34 ± 0.06
	Duration between waves (sec)					
High	$0.80 \pm 0.06 \ (n = 4)$					
Moderate	1.	35 ± 0.21 (n =	10)			
Low	3.	$28 \pm 1.40 (n =$	5)			

Table 1.—Temporal and topological characteristics of waving behavior in *Uca marguerita* from Eastern Mexico.

one individual waving at low intensity expressed two pauses. Pauses at the apex or on the return flexure were never noted. During the upward movement of the claw after the frontal pause, the second and third ambulatories on the minor side and the second on the major may be extended laterally to a position parallel with the substrate. These are returned to supporting positions before the cheliped is brought down to the frontal position (6). The minor cheliped is also flexed laterally after the initial pause and oscillation of the large cheliped.

The wave displays may be classified into three intensities on the basis of duration (Table 1). The highest intensity waves are observed with the approach of a female. These waves are approximately 1.0 s in duration. Low intensity waves are a little more than 2.5 s. The latter were observed when no other crabs were near. The time course of successive waves changes with the approach of another crab. At first, waves are expressed very rapidly and the upward pausing phase (position 2 and 3) is scarcely discernable. As a female approaches, durations are then increased and a bobbing or curtsy (Crane, 1975:496, 658) is incorporated. During this slower waving, the legs may or may not be extended laterally.

The movement of the cheliped from an initial pause to a frontal position at the completion of a wave does not change with increase in waving intensity (Table 1). The complete execution from initial pause to unflexed frontal position occurs in approximately 0.5 s without stop at vertex. Apparently wave duration is determined by the amount of time spent raising the heel and dactyl to a frontal position (1 & 2) and time spent in oscillation pause phase (3). The initial step may vary from 1.66 to 0.41 s while the pause may simultaneously vary from 0.32 to 0.17 s between low and high intensity waving. On the other hand, pauses between successive waves are proportional to wave duration. During high intensity waving, interwave duration is 0.80 s. At intermediate intensity, the interval is increased to 1.35 s while at low intensity there are 3.28 s between waves. The lowest intensity waves are extremely variable in this component.

Discussions and Conclusions

The general morphology of the new species is most closely allied with the fiddler crab subgenus *Minuca* (Crane, 1975). In the Atlantic, this taxon possesses two more or less related superspecies, galapagensis and minax, as well as the species U. burgersi. Of the superspecies, galapagensis possesses frontal breadths less than ¹/₃ carapace width while the minax superspecies and U. burgersi have frontal-carapace relationships exceeding this value. Consequently, Uca marguerita may be distinguished from the broad-fronted western Atlantic Uca mordax, U. pugnax, U. longisignalis, U. vocator, U. burgersi, and U. minax. Moreover, it can be separated from U. mordax and U. longisignalis by a lack of pubescence on the ventral surfaces of ambulatory meral, carpal and propodal segments (Crane, 1975:630–631). Females also lack a genital tubercle, which aids in discerning them from U. mordax, U. pugnax, U. vocator, U. minax and U. longisignalis as well as the narrow-fronted U. rapax.

The Uca pugnax virens of Crane from Mexico (USNM 138645) do not possess the genital tubercle. On the other hand, the only female specimen claimed by Salmon and Atsaides (1968) as a U. virens (USNM 72132) has this structure. Also, the female from Crane's Texas lot (USNM 72131) which is believed to be U. p. virens is equipped with the genital tubercle. The Mexican samples of females discussed by Crane are thus quite distinct from the Texas samples of U. virens, and are considered to be Uca marguerita. By the same token, the largest female of the U. burgersi sample (Holthuis, 1967) from Mexico, in which all lack genital tubercles, possesses a frontal width less than $\frac{1}{3}$ carapace width. This is also U. marguerita.

Of the Atlantic Minuca, U. marguerita was found sympatric with only U. burgersi, U. vocator and U. rapax. The males of the new species are readily distinguished from U. vocator on the basis of absence of pubescence from the carapace and dorsal surfaces of ambulatory meri, a highly developed oblique ridge across the palm of the major cheliped, and a short appearing body. The new species is more difficult to distinguish from the galapagensis superspecies and U. burgersi. However, it may be segregated from U. burgersi by its narrower frontal region, and a more granular, shorter appearing carapace. On the inner surface of the male's large cheliped (Fig. 1B), the tubercles of the superior carina along the upper margin of the cheliped carpal sinus turn toward the dactyl in U. marguerita, but back to

the edge of the cavity in Uca burgersi. On the inner palm, the proximal predactyl ridge is not as arched in U. marguerita as in either U. burgersi or U. mordax. Although U. burgersi and U. marguerita possess similar gonopores, the male gonopods are distinct in their areas of sympatry (Fig. 2). Those in the new species are thinner, more straightened proximately and have a more sharply angled tip than U. burgersi. The cuticular tip is shorter in the new species while the proximal and medial palps appear longer in U. burgersi.

Unfortunately, the general dimensions of the carapace and frontal lobe in males of both Uca rapax and the new species are quite similar. The frontal lobe of the new species is distinctly spatulate as opposed to the angular or truncated lobe of U. rapax. The eyebrows are broader in Uca marguerita than in either U. rapax or U. pugnax. In U. marguerita the eyebrows are horizontally inclined to such a degree that they appear almost as wide as the adjacent eyestalk peduncle. The eyebrows of U. rapax as well as U. virens (Crane, 1975:201) are sufficiently angled so that they are clearly visible in a dorsal carapace view. Since the eyebrows of U. pugnax are nearly vertical in a lateral view they are barely visible from the median dorsal perspective (Rathbun, 1918:395, 398). The cheliped contains tubercles that are large and an arched, proximal predactyl ridge that is distinct from the smooth palm and parallel ridge of male U. rapax or U. virens. The oblique ridge of U. marguerita is developed to a much higher apex than in other local Minuca. The distal extension of the superior carina is also distinct from those found in both U. rapax and U. pugnax. The gonopod of U. rapax is distinctly broader and possesses a more extended cuticular tip than in the new species (Fig. 2). The male gonopod was helpful in identifying the clawless U. marguerita in RMNH 7574.

The waving display of the new species also is distinct from other Atlantic *Minuca*. These are similar to those expressed by other members of the galapagensis superspecies. The duration of single waves in *U. longisignalis*, *U. minax*, *U. pugnax*, *U. vocator* and *U. burgersi* are considerably longer than the waves of the new species. In particular, the duration of the lowest intensity waves in the new species is approximately equal to the high intensity waves of both *Uca rapax* (Salmon, 1967; Crane, 1975) and *U. virens* (Salmon and Atsaides, 1968). Moreover, the ascending portion of waves contains fewer ascending pauses than any other Atlantic *Minuca*. On the basis of ethology, the new species is obviously readily distinguishable in the field.

Relationships.—Although less is known about the Pacific *Minuca*, von Hagen (1968) described in some detail the waving behavior and gonopod structure of both *U. galapagensis* Rathbun and *U. herradurensis* Bott from Peru. These Pacific relatives differ from *U. rapax* and *U. pugnax* by having the palm of the cheliped tuberculate, the oblique ridge of the claw developed

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to a high apex and strong postorbital sulcus on dorsal carapace. Both are moderately narrow-fronted *Minuca* (Crane, 1975:183). The genital tubercle is absent in the female of the Pacific species. The same ensemble of characters may be used to distinguish the new species from its Atlantic relations.

Although the waves of male Uca galapagensis are highly variable, they are distinct from those of U. rapax and U. herradurensis. In U. galapagensis, vibrational components accompany a single apical pause. Although the new species lacks any pause at the vertex, the positioning of the cheliped in front of the mouth parts at the end of a wave, oscillatory movements, and short wave durations in U. marguerita courtship display are reminiscent of the patterns in Uca galapagensis (von Hagen, 1968; Crane, 1975). Consequently, on the basis of similarity in morphology and behavior, Uca marguerita, the new species, tentatively appears to be phyletically close to the Pacific relatives in the Minuca superspecies, galapagensis.

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Literature Cited

- Buitendijk, A. M. 1950. Note on a collection of decapod Brachyura from the coasts of Mexico, including the description of a new genus and species.—Zool. Meded. (Leiden) 30:269– 282.
- Crane, J. 1975. Fiddler Crabs of the World (Ocypodidae; genus Uca).—Princeton University Press, Princeton. 1–736.
- von Hagen, H. O. 1968. Studien an peruanischen Winkerkrabben (Uca).—Zool. Jahrb. System. 95:395–468.
 - —. 1970. Verwandtschaftliche Gruppierung und Verbreitung der karibischen Winkerkrabben (Ocypodidae, Gattung Uca).—Zool. Meded. (Leiden) 44:217–235.
- . 1975. Klassifikation und phylogenetische Einordnung der Lautäusserungen von Ocypodiden und Grapsiden (Crustacea, Brachyura).—Z. f. Zool. System. Evol. 13:300–316.
 . 1980. A key to the "x-species" of North American fiddler crabs (genus Uca).—Zool. Meded. (Leiden) 55:87–96.
- Holthuis, L. B. 1967. On a new species of *Uca* from the West Indian region (Crustacea, Brachyura, Ocypodidae).—Zool. Meded. (Leiden) 42:51–54.
- Rathbun, M. J. 1918. The grapsoid crabs of America.-Bull. U.S. Natn. Mus. 97:1-461.
- Salmon, M. 1967. Coastal distribution, display and sound production by Florida fiddler crabs (genus Uca).—Animal Behav. 15:449–459.

, and S. P. Atsaides. 1968. Behavioral, morphological and ecological evidence for two new species of fiddler crabs (genus *Uca*) from the gulf coast of the United States.— Proc. Biol. Soc. Wash. 81:275-290.

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